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YELLOWS DISEASE OF CELERY, LETTUCE, AND OTHER PLANTS, TRANSMITTED BY CICADULA SEXNOTATA (FALL.)

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INTRODUCTION

Celery affected with yellows was first observed in the San Joaquin delta in 1925 during an investigation of economic plants naturally infected with curly top. During 1926 and 1927 an average of 5 per cent of the crop was affected in the delta, the most important celery producing region in California; in 1928 about 10 per cent of the celery showed symptoms of the disease. Some celery growers hoe out the diseased celery so that an exact percentage of yellows could not be obtained in some fields.

During 1927, 7,000 acres of celery, valued at \$3,096,310, were grown in the San Joaquin delta so that the loss due to yellows amounted to \$154,815. During 1928, 7,400 acres of celery are being grown in the delta, but the value of the crop has not been estimated; the loss due to this disease will probably exceed \$300,000.

Lettuce yellows, known as white-heart or rabbit-ear in New York, and Rio Grande disease in Texas, is a rather serious malady of lettuce. Lettuce yellows is of no economic importance at present in California, but its nature is such as to demand field observations year after year to determine its potential importance.

According to Kunkel⁽⁴⁾ aster yellows "is so serious in many sections of the country that the planting of asters is being restricted or

¹ Assistant Entomologist in Experiment Station.

even abandoned. Aster plots showing 90 to 95 per cent of yellowed plants are not uncommon throughout the eastern United States."

Aster yellows first made its appearance in California during 1925 and in the next three years the disease has spread rapidly through the middle and southern sections of the state. Yellows of flowering plants is already causing some concern to seed and flower growers in certain localities.

An investigation was undertaken to determine whether insects, especially leafhoppers, transmitted this disease to celery. Experiments were conducted to determine the relation of the celery disease to aster and lettuce yellows. The relation of yellows to curly top of sugar beets was also investigated. The characteristics, distribution, flights, food plants, and overwintering stage of the six-spotted leafhopper are discussed in this paper.

NAME OF THE DISEASE

A large number of plant diseases are designated by the term "yellows" some of which belong to the virus diseases, as does the one under consideration, while others are caused by fungus parasites. Kunkel⁽⁵⁾ has experimentally transmitted aster yellows with the six-spotted leafhopper, *Cicadula sexnotata* (Fall.) to more than seventy species of plants in twenty-eight families. Celery yellows has been proven to be identical with aster yellows and should be classified with this disease.

"Yellows" of celery caused by a species of *Fusarium* occurs in Michigan, Indiana, Ohio, Pennsylvania, New York, Massachusetts, Connecticut, and New Jersey but has not been reported from California.

OCCURRENCE OF YELLOWS IN CALIFORNIA

Methods of Introduction into California.—The six-spotted leaf-hopper, Cicadula sexnotata (Fall.) has been known to occur in California for a long time, but the yellows disease which it transmits is a recent introduction into the state. Yellows disease may have been introduced into California through shipments of diseased perennial flowering plants from the Middlewest or East, or through cut flowers brought from the Middlewest or East by the traveling public. Successive migrations of infective six-spotted leafhoppers from the Middlewest to California appear to be entirely out of consideration

as a method of introducing yellows. According to Linford⁽⁶⁾, aster and celery yellows first made its appearance in Utah during 1927. If successive westward migrations of infected leafhoppers had occurred the disease should have made its appearance in Utah first.

Distribution.—In California, celery yellows is known to occur in San Joaquin, Santa Clara and Monterey counties. No attempt has been made to determine whether this disease occurs in the celery districts of Santa Barbara, Los Angeles, Orange, and San Diego counties.

Lettuce yellows occurs in the Santa Clara and Salinas valleys and has been observed by Mr. Ivan C. Jagger, in his experimental summer plantings of letture at Chula Vista.

Smith, who worked with aster yellows in Massachusetts, (11) was first to notice aster yellows at Boulder Creek, Santa Cruz County during 1925; at Berkeley, Alameda County during 1926; and at Arroyo Grande, San Luis Obispo County during 1927. Many shipments of flowering plants, especially asters and zinnias, have been received and proved to be naturally infected with yellows, showing that the present known distribution of this disease is from Sonoma to Los Angeles counties.

PRODUCTION OF NON-INFECTIVE CICADULA SEXNOTATA (FALL.)

Kunkel⁽⁴⁾ found that wheat and rye are immune to asters yellows and that the disease is not transmitted through the egg of *Cicadula sexnotata*.

In order to obtain non-infective Cicadula sexnotata for experimental purposes, adults captured on celery in the field were confined in cages enclosing wheat. After the nymphs hatched from eggs deposited in the wheat, all of the adults were removed from the cages. After the nymphs acquired the winged stage, the males were transferred from wheat to celery, asters, lettuce, and buckwheat. They failed to transmit yellows to these cultivated plants.

A low population of the six-spotted leafhopper was obtained on wheat owing to mildew, and hence Sacramento barley, which is resistant to mildew, was used in subsequent experiments. The six-spotted leafhoppers were collected in the grain field and foothills of the San Joaquin Valley and allowed to oviposit in barley. The insects which developed on barley were not able to transmit yellows.

CELERY YELLOWS

Symptoms.—The first symptoms to appear in celery infected with yellows by the six-spotted leafhopper in the greenhouse is a vertical or upright position of the petioles, which are somewhat longer than those of the healthy leaves of the same age. The petioles of the innermost or youngest leaves are shortened and chlorotic and begin to twist (fig. 1) and intertwine (figs. 2, 3). Celery naturally infected with yellows sometimes shows a circular twist of the petioles (fig. 4). A general yellowing of the plant then develops with a premature blanching of the outer leaves. The vertical or upright petioles gradually assume a flat position. The petioles are brittle, break easily, and often crack (fig. 5). In the later stages of the disease, the heart of the plant decays (fig. 6), forming a soft yellowish brown rot which extends down into the base of the plant.

Incubation Period.—The incubation period of the disease was determined in eighty-seven Golden Self-Blanching celery plants infected with yellows. The six-spotted leafhoppers were fed for a period of two to three weeks or longer on diseased celery or asters removed from the field or on celery or asters experimentally infected with yellows in the greenhouse and were then transferred to healthy celery. Males were used rather than females in order to prevent oviposition. The length of time that elapses from the inoculation of the plant until the petioles began to twist was considered as the incubation period of the disease. The minimum, maximum, and mean incubation periods during the four seasons of the year are given in tables 1 and 2. Celery plants used as a check or control remained healthy.

TABLE 1
INCUBATION PERIOD OF YELLOWS DISEASE IN CELERY INFECTED DURING AUTUMN
AND WINTER

Dates leaf hoppers inoculated plants	Number of celery plants inocu- lated	Number of leaf- hoppers on each plant	Number of plants infected	Number of plants healthy		Maximum incubation period in plant days	Mean incubation period in plant days
Sept. 26-Oct. 6	1	13	1	0	41	41	41.0
Nov. 29-Dec. 11	- 6	2	5	1	43	87	66.0
Dec. 9-17	9 .	3	5	4	38	53	43.8
Dec. 19-29	10	4	6	4	32	57	47.1
Dec. 10-20	4	3	3	1	97*	112	102.0
Dec. 11-21	2	3	2	0	99*	111	105.0
Jan. 3-20	5	10	4	1	30	60	42.2
Jan. 21-Feb. 4	5	6	5	0	34	60	50.0
Total	42		31	11			

^{*} Incubation period in field.



Fig. 1. Celery (Apium graveolens dulce) leaves from a plant infected with yellows in the greenhouse, showing curved petioles.



Fig. 2. Celery (Apium graveolens dulce) plant naturally infected with yellows, showing twisted and intertwined petioles.



Fig. 3. Celery (Apium graveolens dulce) plant inoculated with yellows by infective six-spotted leafhoppers in the greenhouse, showing twisted and intertwined petioles.

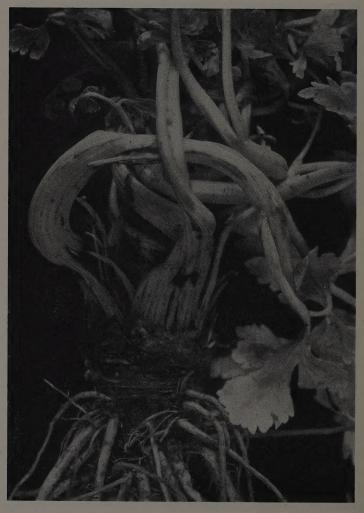


Fig. 4. Celery (Apium graveolens dulce) plant naturally infected with yellows, showing circular twisting of petioles.



Fig. 5. Petioles of celery (Apium graveolens dulce) plant naturally infected with yellows, showing splitting.



Fig. 6. Longitudinal section of celery (Apium graveolens dulce) plant naturally infected with yellows, showing decay of heart leaves.

TABLE 2
INCUBATION PERIOD OF YELLOWS DISEASE IN CELERY INFECTED DURING SPRING AND SUMMER

Dates leaf hoppers inoculated plants	Number of celery plants inocu- lated	Number of leaf- hoppers on each plant	Number of plants infected	Number of plants healthy	Minimum incubation period in plant days	Maximum incubation period in plant days	Mean incubation period in plant days
Apr. 25-May 8	11*	5	10	1	26	63	47.6
May 29-June 12	12	25	11	1	27	59	39.1
June 12-19	12	20	8	4 -	24	34	27.3
June 25-27	12	20	9 .	3	18	32	22.7
June 27-July 9	12	20	8	4	29	50	36.7
July 21-28	12	20	10	2	44	79	56.8
Total	71		56	15			

^{* 11} plants that remained healthy in the incubation trials reported in table 1, inoculated a second time.

It is evident from tables 1 and 2, that the shortest incubation periods occurred in celery infected in late May and during June. All celery infected during May and June was planted and transplanted on the same dates.

According to table 1, eleven celery plants remained healthy and these were inoculated a second time during the spring. Ten of the plants developed symptoms of yellows as indicated in table 2. One plant grew a seed stalk and was rejected, since no study has been made of yellows in seed plants.

Transfer of Yellows from Experimentally and Naturally Infected Celery to Healthy Celery.—Non-infective six-spotted leafhoppers fed on some of the celery experimentally infected with yellows (tables 1 and 2) and then on healthy celery, transmitted the disease to all healthy plants tested. Non-infective hoppers which were fed on healthy celery used as a check or control failed to produce the disease.

Non-infective six-spotted leafhoppers after feeding on thirteen naturally infected Golden Self-Blanching celery plants removed from the field in both early and late stages of the disease transmitted yellows to eight of thirteen healthy celery plants. Golden Heart and Yellow Plume were proved to be naturally infected with yellows.

Varieties of Celery Experimentally Infected with Yellows.—The following varieties of celery (Apium graveolens dulce) have been experimentally infected with the disease: Easy Blanching, Giant Paschal, Golden Self-Blanching (dwarf type and tall or new French type), and White Plume.

Celeriac or Turnip-Rooted Celery (Apium repaceum celeriac).— Celeriac or turnip-rooted celery was experimentally infected with yellows in the greenhouse.

Distribution of Disease in Celery Fields.—Celery affected with yellows was not uniformly distributed in a field, sometimes being more abundant along the margins. The diseased plants sometimes occur in groups scattered over several rows; frequently several adjacent plants in a row are diseased.



Fig. 7. Left, malformed leaf of plantain or ribgrass (Plantago major), showing yellowing. Right, dark green, healthy leaf.

Infection of Celery from Plantain Affected with Yellows (Plantago major).—Plantain or ribgrass (Plantago major) growing in the irrigation furrows between the celery beds at Terminus was proved to be naturally infected with yellows. Non-infective six-spotted leafhoppers after feeding on plantain transmitted yellows to celery and asters. The inner leaves of this diseased weed were often malformed and chlorotic (fig 7) with elongated petioles, while the youngest leaves were



Fig. 8. Left, healthy spike of plaintain or ribgrass (Plantago major). Four spikes on right affected with yellows, three of them showing curling.

reduced in width, being narrow and elongated. The inner spikes were yellow, dwarfed, and sometimes curled (fig. 8). Nymphs and adults of the six-spotted leafhopper were commonly observed on plantain or ribgrass. Nymphs were hatched from eggs deposited in this weed under natural conditions and completed their life history on it in the greenhouse. In all probability, the six-spotted leafhoppers transmitted yellows from plantain or ribgrass to celery, since nymphs and adults were common on celery along the margin of the beds.

Absence of Yellows in Celery Beds.—A number of celery beds were examined in the San Joaquin delta and Salinas Valley but no yellows has been found up to the present time. Some celery growers plant celery after harvesting a crop of potatoes, but celery beds examined as late as July 10, failed to reveal a single plant affected with yellows. As soon as celery plants make a thrifty growth after transplanting, yellows appears. In all probability when the plants are grown close together in the celery beds, the symptoms fail to develop.

Early and Late Planting of Celery.—Celery growers state that early planted celery shows a higher percentage of yellows than late plantings in the San Joaquin delta. In the Santa Clara Valley, however, one celery grower was supplying the local markets with celery during the winter, and repeated examinations of his field showed that 25 per cent of his crop was affected with yellows.

Mechanical Inoculation Tests.—All attempts to transmit yellows to celery by diseased juice inoculations have failed. In one experiment sixty-one healthy celery plants were inoculated with juice extracted from the roots, stems, petioles, or blades of ten naturally infected celery plants, using the flamed needle or capillary tube method of inoculation, but all without effect. In the next experiment forty-two healthy celery plants were inoculated with filtered juice extracted from the roots, stems, and petioles of eight celery plants experimentally infected with yellows. The juice was centrifuged for one hour and filtered through fine Berkefeld candles. A 5 per cent solution of hypophysis was added to some of the diseased juice which was then filtered through fine Berkefeld candles. The filtered juice in sterilized test tubes was capped with a mixture of equal parts of vaseline and paraffin and incubated for a period of from two to ten days before inoculation. It was then injected with a hypodermic syringe into the stem and root of healthy celery plants, but without effect.

ASTER YELLOWS

Smith⁽¹¹⁾ has described the aster yellows disease, especially as it affects the flower, and Kunkel⁽⁴⁾ described the foliage symptoms. A detailed description is not necessary in this paper, but a brief account of the more important symptoms will be given.



Fig. 9. China aster (Callistephus chinensis) affected with yellows, showing upright petioles and dwarfed younger leaves. Non-infective six-spotted leafhoppers, after feeding on diseased celery plants, transmitted yellows to asters.

Symptoms on China Aster.—The first symptom to appear on the youngest leaves of a small plant is a clearing or transparency of the veinlets (pl. 1, figs. 1, 2) with a slight yellowing along them. Diseased leaves are frequently malformed (pl. 1, fig. 2) with somewhat longer, upright petioles (fig. 9). The youngest leaves are dwarfed with shortened petioles and the blades are sometimes reduced to but little more than the diameter of the petioles (fig. 10). Small plants when infected are severely stunted, but the amount of dwarfing of a plant varies with the size of the plant at the time of infection. Secondary shoots frequently grow in the axil of the leaves.

One of the most striking symptoms of aster yellows is the peculiar abnormal development of the flowers. Greenish yellow flowers frequently develop which are often dwarfed (fig. 11). A portion of a flower may show the natural color of the variety while the remaining part may be greenish yellow or white (fig. 12). The secondary shoots arising from the axil of the leaves usually bear no flowers or only small flower heads. Diseased flowers develop an enlargement of the ovaries (pl. 2) but produce little or no seeds.



Fig. 10. Terminal end of two China aster (Callistephus chinensis) plants affected with yellows, showing dwarfed youngest leaves with shortened petioles. The youngest leaves of the plant on the right have blades reduced to but little more than the diameter of the petioles.

Transfer of Celery Yellows to China Aster.—Non-infective six-spotted leafhopper after feeding on experimentally and naturally infected celery transmitted the disease to healthy China asters. Non-infective hoppers after feeding on asters experimentally infected with yellows transmitted the disease back to healthy asters and celery. When non-infective leafhoppers were transferred from healthy celery or asters to aster plants, yellows did not develop. This experiment proves that the virus of celery and aster yellows are identical.



Fig. 11. Center: normal flower, from a China aster (Callistephus chinensis) plant to which non-infective six-spotted leafhoppers failed to transmit the disease from healthy celery. Grouped around it are four dwarfed aster flowers which were greenish yellow in color, from a plant infected with yellows by the six-spotted leafhopper, transferred from diseased field celery.



Fig. 12. Center: normal flower, from a China aster (Callistephus chinensis) plant to which non-infective six-spotted leafhoppers failed to transmit the disease from healthy celery. Grouped around it are four flowers showing abnormal portion which was greenish white or white, while the normal part retained the natural color of the variety; from aster plants inoculated with yellows by non-infective six-spotted leafhoppers after feeding on celery infected with the disease in the greenhouse.

Incubation Period.—The first symptom of aster yellows to develop, namely, the cleared or transparent veins, appeared in from 11 to 27 days in small plants, with an average period of 18.3 days in the greenhouse, as indicated in table 3.

 ${\bf TABLE~3}$ Incubation Period of Yellows Disease in Asters in the Greenhouse

Aster plant No.	Dates C. sexnotata inoculated plants	Date transparent venation developed	Incubation period in plant days
1	Jan. 14	Feb. 5	22
2	Feb. 2	Feb. 19	17
3	Feb. 6	Feb. 19	13
4	Feb. 6	Feb. 19	13
5	Feb. 6	Feb. 26	20
6	Feb. 6	Feb. 26	20
7	Feb. 6	Feb. 26	20
8	Mar. 11	Mar. 30	19
9	Mar. 27	Apr. 23	27
10	Apr. 7	Apr. 18	11
11	Apr. 7	Apr. 27	20
Average			18.3

YELLOWS OF OTHER FLOWERING PLANTS

Zinnia.—A circular bed of zinnias (Zinnia elegans) showing 100 per cent yellows was found in the center of a lawn in front of the Spreckels Agricultural Experiment Station. The six-spotted leaf-hopper was abundant on the zinnias and on the grass. The plants were stunted, chlorotic, and with abnormal flowers (fig. 13). Non-infective leafhoppers after feeding on the diseased zinnias transmitted yellows to asters and celery. A shipment of zinnias was also received from San Gabriel, Los Angeles County, and these were also proved to be naturally infected with yellows. Zinnias grown from seeds were also experimentally infected with the disease.

African Marigold.—African marigold (Tagetes erecta) was demonstrated to be naturally infected with yellows in Berkeley. The plants were stunted and yellow and failed to blossom.

A list of flowering plants naturally and experimentally infected with yellows and curly top will appear in a future paper.



Fig. 13. Malformed flowers of Zinnia elegans affected with yellows.

LETTUCE YELLOWS (WHITE-HEART, RABBIT-EAR, OR RIO GRANDE DISEASE OF LETTUCE)

Kunkel⁽³⁾ considers aster yellows identical with a serious malady of lettuce (*Lactuca sativa*) known as white-heart or rabbit-ear in New York and Rio Grande disease in Texas.

The variety of lettuce known as New York or Los Angeles was proved to be naturally infected with yellows in the Santa Clara and Salinas valleys. Non-infective six-spotted leafhoppers were fed for a few days on diseased lettuce removed from the field and were then transferred to healthy lettuce, celery, and asters, and all developed typical symptoms of yellows.

Lettuce yellows was rare in the Santa Clara Valley. An examination of the lettuce fields in the Salinas Valley was made on June 7–8, 1928, and lettuce affected with yellows was found here and there in a few rows adjacent to alfalfa and barley fields, but the disease was rare away from the margin of the lettuce fields. The six-spotted leaf-hopper was abundant in alfalfa and barley fields and was common in the lettuce fields. In the Watsonville district, lettuce yellows was somewhat more abundant than in the Salinas district, but the disease cannot be considered of economic importance at present.

Symptoms.—Lettuce affected with yellows before heading is readily detected at a short distance in the field by the yellow color of the outer leaves, the blanched appearance of the heart leaves, and a stunting of the plant (pl. 3). The blanched inner or youngest leaves are dwarfed and the blades are often reduced to but little more than the petioles (fig. 14). In lettuce infected before heading, the heart leaves curl outward instead of inward and form no heads (pl. 4).

Lettuce affected after heading showed the dwarfed blanched heart leaves (pl. 5), which fail to form a solid head. Brown spots occur along the margin of the heart leaves (fig. 15), and sometimes the tips of the central dwarfed leaves are entirely brown (fig. 15).

Experimental Infection.—New York or Los Angeles lettuce experimentally inoculated with yellows by infective male Cicadula sexnotata in the greenhouse was transplanted in the field together with check or control plants on which non-infective leafhoppers had fed. The infected lettuce developed symptoms similar to those of naturally infected plants, while the check or controls remained healthy.



Fig. 14. Leaves from New York or Los Angeles lettuce (Lactuca sativa) plant inoculated with yellows by infective six-spotted leafhoppers, showing outward cupping of larger leaves, and dwarfing of smaller leaves with blades reduced to but little more than the petioles.



Fig. 15. Brown spots on heart leaves of New York or Los Angeles lettuce (Lactuca sativa) affected with yellows. Left, lower row: tips of two dwarfed leaves entirely brown.

Lettuce experimentally inoculated with yellows by infective six-spotted leafhoppers in the greenhouse assumed a spindling habit and developed many short upright flowering branches. The infected plants were chlorotic and showed the transparent veinlets on the younger leaves, although these cleared veinlets were often difficult to distinguish from normal venation of the leaves in the check or control plants. Non-infective six-spotted leafhoppers were fed for a few days on the experimentally infected lettuce and were then transferred to healthy lettuce, celery, and asters; all developed typical symptoms of yellows.

Varieties Experimentally Infected.—The following varieties of lettuce were experimentally infected with yellows: Big Boston, Chicken, Early Curled Simpson, Iceberg, New York or Los Angeles, Prizehead, Paris White Cos (Romaine, Cos, or Celery lettuce), and Wonderful.

SIX-SPOTTED LEAFHOPPER, CICADULA SEXNOTATA (FALL.)

Characteristics.—The adult insects (pl. 6, fig. 5) of the spring and summer broods are greenish yellow. A few specimens taken on the foothills of the Santa Clara Valley on February 28, 1928, possessed a faded light brown color pattern resembling in color somewhat the dark overwintering beet leafhoppers (pl. 6, figs. 1–4) near the end of their natural life. The adults are easily recognized by the six black spots (pl. 6, fig. 5) on the vertex of the head, and the front has a double series of black arcs.

The nymphs after hatching develop a dusky color, and in later instars, the general color varies from yellow to light brown, or light greenish-gray.

Distribution.—According to Osborn⁽⁷⁾ the widely distributed six-spotted leafhopper was described in Europe more than a century ago. Uzel⁽¹⁰⁾ reported this species as injurious to sugar beets in Bohemia. Ellinger⁽²⁾ records it as injurious to wheat, oats, and barley in Sweden. According to Junger,⁽³⁾ it is well known throughout Germany as the cause of severe injury to grasses, cereals and certain legumes. Kunkel⁽⁴⁾ states that it occurs in Japan and probably throughout the Orient.

Osborne⁽⁹⁾ found a specimen of *Cicadula sexnotata* in the Harris collection in the Boston Society of Natural History probably collected

between 1840 and 1850, but there was no published record of its occurrence in the country prior to 1884, a fact that very naturally suggests that it might be an introduced species. It is now widely distributed in North America from Alaska to Florida and from Maine to California.

The six-spotted leafhopper is generally distributed in California. Specimens were collected as far south as Calexico in the Imperial Valley as follows: April 2, 1918, on pepper grass (*Lepidium medium*) *Malva* sp. and *Rumex* sp.; in Heber, April 3, 1918, on wheelscale (*Atriplex elegans*). During the past ten years it has been taken on pasture grasses on the plains and foothills of the San Joaquin Valley, also on the foothills bounding the Salinas and Santa Clara valleys.

Flights.—Field observations made in the San Joaquin and Santa Clara valleys during the winter and spring of 1928, indicate that the six-spotted leafhopper flies into the cultivated areas after the pasture vegetation becomes dry on the plains and foothills. Spring brood adults were common during March in fields of barley and oats adjacent to the foothills in the San Joaquin Valley, but during the middle of April, after the grain begins to ripen, the adults fly to other food plants.

Food Plants—The six-spotted leafhopper has a wide range of food plants in the United States and is a pest to forage, cereal, garden crops, and flowering plants. Osborn (*) found it abundant in meadow and marsh grasses and pastures, and common on timothy in Maine. It migrates to grain fields and is a serious pest to oats. After the oats ripen it spreads to adjacent potato and corn fields. Kunkel found that Cicadula sexnotata will live and reproduce on "aster, lettuce, sow thistle, great ragweed (Ambrosia trifida L.) daisy fleabane (Erigeron annuus (L.) Pers.) and other Erigerons, English plantain (Plantago lanceolata L.) dandelion (Taraxacun officinale Weber), wheat, oats, rye, barley calendula, Ammobium alatum, Matricaria alba, Centaurea imperialis, Gaillardia grandiflora, Moon Penny daisy (Chrysanthemum leucanthemum), and the African daisy (Dimorphotheca aurantiaca).''(4)

Life History on Celery.—The six-spotted leafhopper completed its life cycle on young and half-grown Golden Self-Blanching celery plants, but older plants are unfavorable for the multiplication of this insect.

Mortality on Celery.—A high mortality of the adults occurs on large celery plants. In one experiment 120 adults were distributed on sixteen large celery plants enclosed in cages on December 4, and only 25 adults were alive on February 4. As there was a possibility that the leafhoppers were at the end of their natural life, another experiment was performed.

Two small celery plants about transplanting size and two large celery plants were enclosed in four cages, each containing 25 male or female leafhoppers. The mortality at intervals of five or ten days is shown in table 4.

TABLE 4

Comparison of Mortality of Six-Spotted Leafhoppers on Large and Small

Celery Plants

	Ma	ales	Females		
Dates	On large plant	On small plant	On large plant	On small plant	
June 2	25	25	25	25	
June 12	2	17	10	18	
June 22	1	15	5	11	
June 27	1	13	1	9	
July 2	0	12	1	8	
July 7	0	9	0	6	

Life History on Lettuce.—Nymphs which hatched from eggs deposited by the six-spotted leafhopper in the following varieties of lettuce completed their life cycle on these host plants in the greenhouse: Big Boston, Chicken, Early Curled Simpson, Iceberg, New York or Los Angeles, Prizehead, Paris White Cos (Romaine, Cos, or Celery lettuce), and Wonderful.

Overwintering Stage.—Experiments conducted by Kunkel⁽⁴⁾ give indirect proof that the six-spotted leafhopper passes the winter in the egg stage in New York. This leafhopper winters over in the adult stage in California, deposits its eggs, and is at the end of its natural life in March. Nymphs in the last instar were taken on the foothills of the Santa Clara Valley on February 28, 1928. A few females with a faded light brown color pattern were also taken, but these died in a few days on asters. Adults were also taken during December, 1928, and January, 1929, wintering on the foothills and in the cultivated areas of the Salinas Valley.

Transmission Experiments with Sugar-Beet Curly Top.—The six-spotted leafhopper is not able to transmit curly top. Non-infective Cicadula sexnotata after feeding on curly-top beets failed to communicate this disease to celery plants, asters, and beets. Non-infective six-spotted leafhoppers did not transmit curly top from two celery plants experimentally infected with the disease to healthy beets.

Life History and Longevity on Sugar Beets.—The six-spotted leafhopper was not able to complete its life history on sugar beets. The longevity of the last living male and female leafhopper was determined with different lots of adults feeding on small and large beets as follows:

Sugar beets	Longevity of males days	Longevity of females days
2-4 leaves	2-11	2-4
8-10 leaves	7 .	60
12-16 leaves	22	62
4 months old	14	18

It is evident that the adult life of the males was shorter than the females on all beets except those with 2-4 leaves.

EXPERIMENTS WITH BEET LEAFHOPPER, EUTETTIX TENELLUS (BAKER)

Investigations conducted in the celery fields in the San Joaquin delta regions and in the vegetable gardens of the Spreckels ranches in the Salinas Valley during the 1925 outbreak of the beet leafhopper, Eutettix tenellus (Baker), demonstrated that this insect was occasionally taken on celery. In years between outbreaks of the pest, this leafhopper was rarely found on celery. During the spring of 1927 the beet leafhopper migrated over the Coast Range from the San Joaquin into the Salinas and Santa Clara valleys, and an occasional adult, but rarely a nymph, dropped to the ground when celery was shaken during the summer.

A large number of celery plants were removed from the field during 1925-27, but, up to the present time, celery has not been demonstrated to be naturally infected with curly top.

Carsner $^{(1)}$ states that celery ($Apium\ graveolens$) is non-susceptible to curly top.

Golden Self-Blanching celery was inoculated with curly top by ten infective beet leafhoppers in the greenhouse but only two of eighteen plants were experimentally infected with the disease. Different lots of non-infective beet leafhoppers after feeding on the two plants infected with curly top were transferred to healthy beets and typical symptoms of the disease developed. In one celery plant infected with curly top during April, the virus remained active during May and June, while from the second celery plant the disease was repeatedly transmitted to beet seedlings for a period of six months and at the present writing the virus is still active. Celery experimentally infected with curly top showed a shortening of the petioles of the central leaves but the petioles failed to twist and intertwine as in celery yellows. The infected plants showed the transparent veinlets on the youngest leaves, but these cleared veinlets were difficult to distinguish from normal venation in the check or control plants.

Giant Paschal and White Plume celery were also inoculated with curly top by ten infective beet leafhoppers but two of six plants of the former variety, and one of six plants of the latter variety were experimentally infected with the disease.

Nymphs which hatched from eggs deposited by the beet leafhopper in Giant Paschal, Golden Self-Blanching, and White Plume celery completed their life cycle in the greenhouse.

The beet leafhopper is not able to transmit yellows and the beet is immune from this disease. Non-infective beet leafhoppers after feeding on celery and asters affected with yellows failed to transmit this disease to healthy celery plants, asters, and beets. Healthy beets were repeatedly inoculated with yellows by different lots of infective six-spotted leafhoppers for a period of three weeks, but non-infective Cicadula sexnotata or Eutettix tenellus after feeding on the inoculated beets failed to transmit this disease to healthy celery plants, asters, and beets.

Asters were repeatedly inoculated with curly top by different lots of infective beet leafhoppers but asters were found to be immune from this disease.

Nymphs which hatched from eggs deposited by the beet leafhopper in asters failed to complete their life history in the greenhouse. The males lived from 3 to 11 days and the last female died at the end of 17 days on asters.

The following varieties of lettuce were demonstrated to be immune to curly top: Big Boston, Chicken, Early Curled Simpson, Iceberg, New York or Los Angeles, Prizehead, Paris White Cos (Romaine, Cos, or Celery lettuce), and Wonderful. The beet leafhopper failed to complete its life cycle on the above varieties of lettuce.

EXPERIMENTS WITH AGALLIA CALIFORNICUM (BAKER), A. CINEREA (O. & B.), AND EMPOASCA FLAVESCENS (FAB.)

An examination of the insect population on celery was made during 1925 and in later years. Several other species of leafhoppers were often taken on celery. Nymphs and adults of Agallia californicum (pl. 6, fig. 6), A. cinerea, and Empoasca flavescens (pl. 6, fig. 7), were taken on celery in the field. The three species of leafhoppers completed their life cycle on celery in the greenhouse and many generations were reared.

Adults of each species bred on celery affected with yellows were transferred to healthy celery and aster plants, but in no case did they transmit the disease.

SUMMARY

The data presented in this paper prove that the six-spotted leaf-hopper Cicadula sexnotata (Fall.), transmits yellows disease to celery. Non-infective six-spotted leafhoppers reared on barley failed to produce the disease in healthy celery. The disease was transferred by non-infective leafhoppers feeding on celery experimentally infected in the greenhouse back to healthy celery. Non-infective leafhoppers after feeding on naturally infected celery transmitted yellows to healthy celery plants.

It was demonstrated that yellows of celery is identical with aster yellows. Non-infective six-spotted leafhoppers after feeding on experimentally and naturally infected celery transmitted yellows to asters. Non-infective hoppers after feeding on asters experimentally infected with yellows transmitted the disease back to healthy celery and asters.

It was also shown that yellows of celery and asters is identical with lettuce yellows, which is also known as white-heart, rabbit-ear, or Rio Grande disease.

A number of flowering plants of the Compositae, such as China asters, zinnias, and African marigold, were proven to be naturally infected with yellows. Plantain or ribgrass (*Plantago major*) was also demonstrated to be naturally infected with yellows.

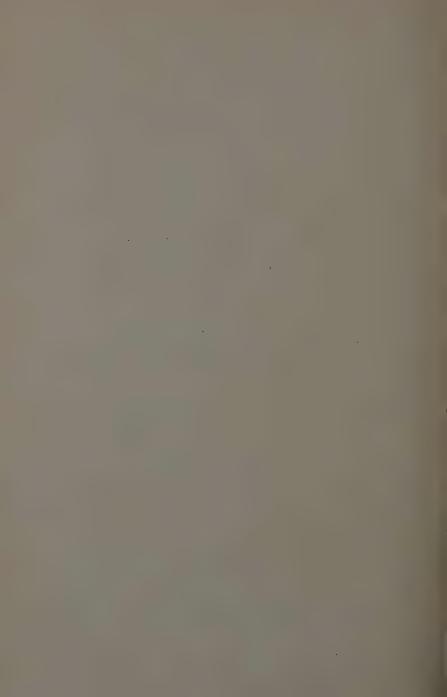
Celery and aster yellows first made its appearance in California during 1925, and in four years has spread from Sonoma to Los Angeles counties.

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PLATES 1-6

China Aster (Callistephus chinensis)

- Fig. 1. Clearing or transparency of the veins on left half of leaf affected with aster yellows.
- Fig. 2. Malformed and dwarfed leaves of asters affected with yellows, showing the clearing and transparency of the veins on a portion of the blade.





Fig. 2

Fig. 1

China Aster (Callistephus chinensis)

Longitudinal sections of aster flowers: center, from a healthy plant; others, from diseased plants showing enlarged ovaries.



New York or Los Angeles Lettuce (Lactuca sativa)

Upper, healthy lettuce head. Two lower lettuce plants were naturally infected with yellows, also known as white-heart, rabbit-ear, or Rio Grande disease. The two stunted plants were transplanted on the same date as the healthy one.



New York or Los Angeles Lettuce (Lactuca sativa)

Lettuce plant naturally infected with yellows, showing dwarfed youngest leaves, and outwardly curled older leaves. This is the same plant as that shown in the lower left-hand corner of plate 3, enlarged to show the symptoms.



PLATE 5 '

New York or Los Angeles Lettuce (Lactuca sativa)

Longitudinal sections of lettuce heads: upper, healthy; lower, naturally infected with yellows, showing dwarfed, outward-curled, central leaves.



- Figs. 1–4. Beet leafhoppers, Eutettix tenellus (Baker), dark overwintering adults.
- Fig. 5. Six-spotted leafhopper, $Cicadula\ sexnotata\ (Fall.),\ spring\ broad\ adult.$
 - Fig. 6. Agallia californicum (Baker).
 - Fig. 7. Empoasca flavescens (Fab.).

